

Vampyressa pusilla.

By Susan E. Lewis and Don E. Wilson

Published 12 August 1987 by The American Society of Mammalogists

Vampyressa Thomas, 1900

Vampyrops (*Vampyressa*) Thomas, 1900:270. Type species *Phyllostoma pusillum* Wagner, 1843, by original designation.
Vampyressa Miller, 1907:156, first use of name in generic sense.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Stenodermatinae. The genus *Vampyressa* contains five species in two subgenera. The subgenus *Vampyressa* contains *V. melissa* and *V. pusilla*; the subgenus *Vampyriscus* contains *V. bidens*, *V. nymphaea*, and *V. brocki*. A key to the species follows (Peterson, 1968):

- 1 One pair lower incisors *V. bidens*
Two pair lower incisors 2
- 2 (1) Third lower molar present *V. melissa*
Third lower molar absent 3
- 3 (2) Second lower molar approximately as long as wide with
high anterior and posterior cusps *V. pusilla*
Second lower molar longer than wide with low anterior
and posterior cusps 4
- 4 (3) Forearm in adults more than 34 mm, greatest length of
skull more than 20 mm *V. nymphaea*
Forearm in adults less than 34 mm, greatest length of
skull less than 20 mm *V. brocki*

Vampyressa pusilla (Wagner, 1843)

Little Yellow-eared Bat

Phyllostoma pusillum Wagner, 1843:173. Type locality "Sapitiba," Rio de Janeiro, Brazil.

Vampyressa pusilla, Miller, 1907:156, first use of current name combination.

Vampyressa thyone Thomas, 1909:231. Type locality "Chimbo, near Guayaquil, Ecuador. Alt. 1,000'."

Vampyressa minuta Miller, 1912:25. Type locality "Cabima, Panama."

Vampyressa venilla Thomas, 1924:533. Type locality "San Lorenzo, 500'," Perú.

Vampyressa nattereri Goodwin, 1963:16. Type locality "probably Ipanema, district of São Paulo, Brazil."

CONTEXT AND CONTENT. Context as above. Goodwin (1963) recognized three subspecies of *V. pusilla*: *V. p. pusilla*, *V. p. thyone*, and *V. p. venilla*. Subsequently, Handley (1966:767) regarded *V. pusilla* as monotypic and described the subspecies characteristics as "age rather than geographic variables." In a more recent review of the species, Peterson (1968) recognized two subspecies, *V. p. thyone* and *V. p. pusilla*.

DIAGNOSIS. *Vampyressa pusilla* usually can be distinguished from *V. bidens* by the number of lower incisors. Usually *V. bidens* has one on each side, but *V. pusilla* has two on each side, although Davis (1975) found two individuals of *V. bidens* from Perú with additional lower incisors. In *V. pusilla*, the third lower molar is absent, whereas it is present in *V. melissa* and *V. bidens*.

In two of the five species of *Vampyressa*, the tragus is hirsute on the lateral attachment; *V. pusilla*, *V. melissa*, and *V. nymphaea* lack this plosity. The medial, distal extension of the tragus is finely serrated and more pronounced in *V. pusilla* and smooth and less pronounced in *V. nymphaea* and *V. melissa* (Peterson, 1968).

Vampyressa pusilla and *V. melissa* lack the dorsal stripe present in the other three congeners. The dorsal pelage of *V. pusilla* is paler and the facial markings not as well defined as those of the other species.

The interfemoral membrane of *V. pusilla* is narrower than that of *V. nymphaea* and *V. brocki*. The edge is nearly naked with

the exception of a small fringe in the center. The interfemoral membrane of *V. melissa* is more hirsute (Goodwin, 1963).

The forearm length of *V. pusilla* ranges from 30 to 32 mm (Goodwin, 1963), shorter than that of *V. melissa* and *V. nymphaea* (average forearm lengths 38 and 36 mm, respectively; Peterson, 1968).

GENERAL CHARACTERISTICS. Goodwin (1963:15) described *V. pusilla thyone* (Fig. 1) as follows: "Upper parts anteriorly Pinkish Buff grading to Sacardo's Umber or Sayal Brown on lower back; under parts rather darker than Light Buff; facial stripes white, the upper pair extending back to between ears. Skull with a short, broad rostrum, large, full braincase; upper incisors very unequal, the inner more than twice as high as outer; cutting edges bifid, separated by a space and converging distally but not in contact at tip; upper molars broader than long; lower incisors small, completely filling space between canines, their cutting edges faintly trifid." The skull (Fig. 2) is typical for the subfamily, and the dental formula is $i\ 2/2$, $c\ 1/1$, $p\ 2/2$, $m\ 2/2$, total 28 (Miller, 1907).

Baker et al. (1973), found no significant geographic differences among specimens from Central and South America for one external and eight cranial measurements. Mean and range (in parentheses) of external and cranial measurements (in mm) for 36 specimens from Colombia, Venezuela, and Ecuador are (Baker et al., 1973): length of forearm, 31.4 (29.3 to 33.2); greatest length of skull, 18.4 (17.5 to 19.3); zygomatic breadth, 10.7 (10.0 to 11.3); post-orbital breadth, 4.6 (4.3 to 5.0); breadth of braincase, 8.2 (7.5 to 8.7); mastoid breadth 9.1 (8.6 to 9.6); length of maxillary tooththrow, 5.8 (5.4 to 6.3); palatal length, 8.3 (7.7 to 9.0); breadth across upper molars, 7.7 (7.1 to 8.3). LaVal and Fitch (1977) reported the average mass for 27 specimens from La Selva, Costa Rica, to be 8.2 g.



FIG. 1. *Vampyressa pusilla thyone* from Costa Rica. Photograph by Richard K. LaVal.



FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral and dorsal views of mandible, of male *Vampyressa pusilla pusilla* from Vicosa, Minas Gerais, Brazil (USNM no. 395703). Greatest length of skull is 19.6 mm.

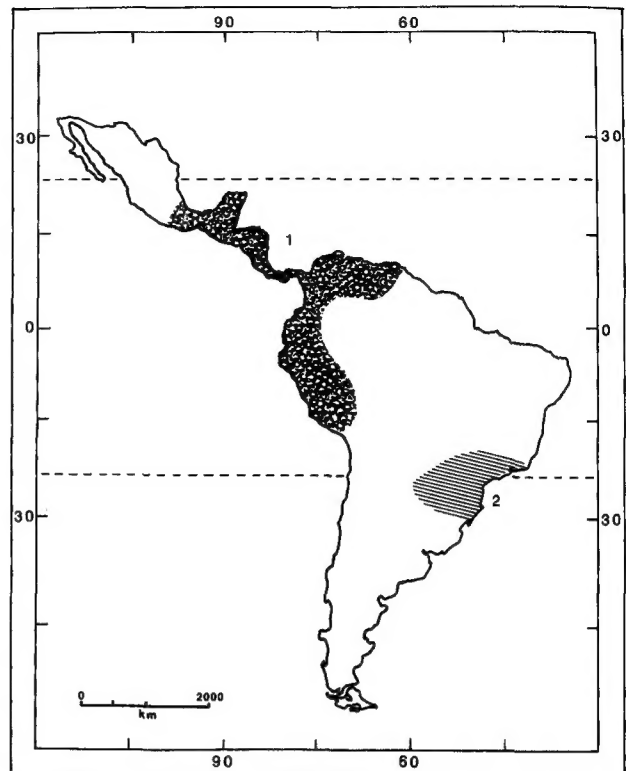


FIG. 3. Distribution of *Vampyressa pusilla*: 1, *Vampyressa pusilla thyone*; and 2, *Vampyressa pusilla pusilla*.

DISTRIBUTION. *Vampyressa p. thyone* ranges from southern Mexico (Oaxaca, Chiapas, Yucatan, Veracruz, and Campeche; Ramirez et al., 1983) south along the Caribbean coast of Central America through Guatemala, Belize (British Honduras), Honduras, Nicaragua, Costa Rica, and Panamá, then east through Colombia (Aellen, 1970) and Venezuela (Handley, 1976) and south through Ecuador and Perú (Fig. 3). *V. p. pusilla* is found in eastern Paraguay (Myers et al., 1983) and southeastern Brazil (Taddei, 1979). There is no fossil record for the species.

Koopman (1978) classified *V. pusilla* as both an Amazonian highland and lowland species in Perú, based on capture records above and below 1,000 m. Graham (1983) gave the elevational limits for 10 specimens of *V. pusilla* from Perú as 300 to 1,500 m. Handley (1976) reported an elevational range in Venezuela of 23 to 1,537 m, with 86% caught above 500 m. Specimens from Panamá in the National Museum of Natural History were taken from sea level to 854 m.

A specimen of *V. pusilla* was reported on a ship passing through the Bass Strait between Australia and Tasmania. Presumably the bat had boarded the vessel when it passed through the Panamá Canal (Hill and Smith, 1984).

FORM AND FUNCTION. In describing the gastric morphology of *V. pusilla*, Forman (1973) noted that the stomach closely resembles that of *Uroderma*, except for an extremely small cardiac vestibule. The stomach has an elongated pouch between the gastroesophageal junction and the left lateral terminus, which Forman (1973) designated as the fundic caecum. This caecum, along with a moderate terminal portion and small cardiac vestibule, gives the stomach a tubular appearance. The rugae are distributed diagonally in the fundic caecum and longitudinally within the remaining portions.

Brunner's glands are absent (Forman, 1971). The zone of pyloric glands in the terminal portion of the stomach is more extensive than in most stenodermines. Forman (1973) suggested that the pyloric mucosa produces an acid-neutralizing agent to protect the upper duodenum from ulceration.

Studier and Wilson (1983) reported average natural urine concentration of 359 mOsm/kg for two females from Panama. Sodium concentration was 5 mEq/l and potassium was 33 mEq/l. All of these values are low for bats in general and even for

frugivorous bats as well (mean natural urine concentration for 148 samples of 13 species, 557 mOsm/kg; Studier and Wilson, 1983).

McDaniel (1976), in describing the external anatomy of the brain, noted that the cerebrum is smooth with well-developed sulci and not domed, as in *V. nymphaea*. The inferior colliculi are exposed dorsally and the pseudotemporal lobes project ventrally at an angle. The cerebellum is simple with a low medial crest.

As part of a comprehensive study of the morphometrics of chiropteran wings, Smith and Starrett (1979) listed the mean overall aspect ratio for five specimens of *Vampyressa* (species not given) as 5.88 and the mean wing loading as 11.50 newtons/m².

ONTOGENY AND REPRODUCTION. Wilson (1979) suggested that the reproductive pattern of *V. pusilla* probably was bimodal polyestry, although data were incomplete. Pregnant females have been collected in January (Fleming et al., 1972), February (Jones et al., 1973; LaVal and Fitch, 1977), March (Jones et al., 1971), April (Fleming et al., 1972; LaVal and Fitch, 1977), June (Myers et al., 1983), July (Davis et al., 1964; LaVal and Fitch, 1977; Rick, 1968; Starrett and de la Torre, 1964) August (LaVal and Fitch, 1977; Valdez and LaVal, 1971), and November (Davis and Dixon, 1976). Lactating females have been collected in March (Fleming et al., 1972), April (Hall and Jackson, 1953), May (LaVal and Fitch, 1977) July, and August (Armstrong, 1969).

Peterson (1965:676) reported a 28 mm, 3.2 g embryo collected on 17 March in British Honduras that was "not quite full term." This exceeded one-half the length of the mother and approached one-half of her mass. These measurements suggest that *V. pusilla* has one of the highest offspring-to-mother size ratios of any species, but animals from Panama average about 10 g, which would provide the more normal ratio of about one-fourth.

ECOLOGY. Handley (1976:29) provided the following details on habitat use based on a collection of 115 specimens from Venezuela: "Caught in mist nets (99 percent) and by hand in a house (1 percent); near streams (5 percent) and other moist areas (73 percent), as well as in dry sites (22 percent); usually in evergreen forest (92 percent), and rarely in yards (5 percent), orchards (1 percent), croplands (1 percent), and swamps (1 percent) . . ." *V. pusilla* also was collected over streams in gallery forests in Nicaragua (Jones et al., 1971), and in dense rainforests in Costa Rica (LaVal and Fitch, 1977). To account for the low incidence of recapture data for *V. pusilla*, LaVal and Fitch (1977) postulated that the species is either nomadic or has a proficiency for avoiding traps and mist nets after the first capture.

Vampyressa pusilla typically is found in the presence of *Artibeus*, *Carollia*, *Sturnira*, *Vampyrops*, and other species of *Vampyressa* (Davis, 1975; Davis and Dixon, 1976; Myers et al., 1983). Although this species is relatively rare, locally dense concentrations have been reported (Davis and Dixon, 1976).

Bonaccorso (1979) captured this species more frequently between 3 and 12 m than at ground level. He also frequently captured them along creeks on Barro Colorado Island in Panama.

Gardner (1977b) summarized the feeding habits of *V. pusilla* as totally frugivorous. They have been found with small amounts of plant material in their stomachs (Fleming et al., 1972; Starrett and de la Torre, 1964). Howell and Burch (1974) identified fruit from guano and stomach contents of *V. pusilla* to be that of *Acnistus* sp., a fruit-bearing tree cultivated near the collection site. Bonaccorso (1979) characterized the species as a common fig specialist, and reported 92% *Ficus yoponensis* in 13 fecal samples.

Webb and Loomis (1977) listed *V. pusilla* as host for four families of mites (Sarcoptidae, *Chirnyssoides caparti*; Macronyssidae, *Macronyssoides* sp.; Spinturnicidae, *Periglischrus iheringi*; and Trombiculidae, *Trombicula dunnii*), and one family of bat fly (Streblidae, *Neotrichobius delicatus*).

Periglischrus iheringi and *Trombicula dunnii* were identified from *V. pusilla* in Panamá (Brennan and Yunker, 1966; Furman, 1966). *Neotrichobius delicatus* was reported from Venezuelan *V. pusilla* by Wenzel (1976) and Wenzel et al. (1966) described *Neotrichobius stenopterus* in part from Panamanian *V. pusilla*. Reed and Brennan (1975) reported *Odontacarus tubercularis* (Trombiculidae) from *V. pusilla* in Venezuela, and Brennan and Reed (1975) added *Crotiscus desdentatus* and *Loomisia desmodus* (both Trombiculidae), also from Venezuela.

BEHAVIOR. Davis and Dixon (1976) recorded nocturnal activity patterns of a population of *Vampyressa pusilla* near Iquitos,

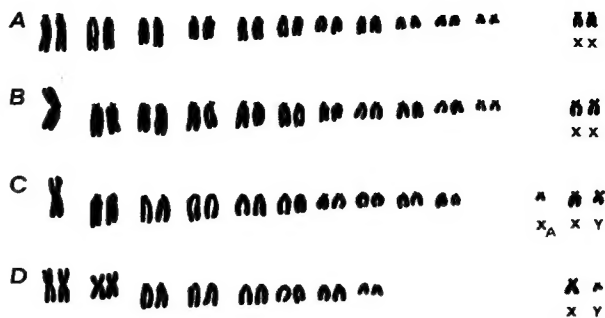


FIG. 4. Representative karyotypes of *Vampyressa pusilla* thylene (Gardner, 1977a). A) $2n = 23-24$, $FN = 22$; female; Villavicencio, Intend. Meta, Colombia; USNM 507191. B) $2n = 22-23$, $FN = 22$; female; Santa Elena, Dept. Huánuco, Peru; LSUMZ 14235. C) $2n = 22-23$, $FN = 22$; male; Santa Elena, Dept. Huánuco, Peru; LSUMZ 14234. D) $2n = 18$, $FN = 20$; Central America (Baker et al., 1973).

Perú, where most captures occurred between 1830 and 2000 h, although bats were captured occasionally throughout the night. Bonaccorso (1979) also found them more active during the first 2 h after sunset.

The roosting habits of *V. pusilla* are not well known. Davis and Dixon (1976) reported that they did not use buildings of a nearby village for daytime roosts, although the species was found in unusually high concentrations in and near the village. Hall and Jackson (1953: 645) disturbed a female *V. pusilla* when they, "had pushed aside bushes that partly obstructed the trail." Timm (1984) reported a single male *V. pusilla* roosting under a cut *Philodendron* sp. leaf in Costa Rica. The bat presumably had cut the veins of the leaf near the base, causing (p. 167), "the entire margin of the leaf to collapse downward forming a pyramid-shaped tent." Similar construction of tents by other species of bats has been reported (Timm, 1984).

GENETICS. Two chromosomal races of *V. pusilla* were described by Baker et al. (1973). The first, from Honduras and Nicaragua, has a diploid number ($2n$) of 18 and a fundamental number (FN) of 20, apparently with an XX/XY sex-determining system (Fig. 4). Six pairs of autosomes are acrocentric and two are metacentric or submetacentric. The X chromosome is small and subtelocentric; and Y is the smallest chromosome of the complement and has a small second arm. A second chromosomal morph, from Colombia, is radically different, with $2n = 24$ in females and $2n = 23$ in males (Fig. 4). The FN is 22 if all autosomes are considered unpaired. Two pairs of autosomes have small, distinct second arms. There are no metacentric or submetacentric autosomes. In males three chromosomes in the complement are distinctly different from others in size and shape. This signifies a sex-determining system other than XX/XY.

Baker et al. (1973) also showed that these chromosomal differences were not reflected in morphology. There was no significant geographical variation for one external and eight cranial measurements.

The Colombian chromosomal morph of *V. pusilla* is similar to that of *Mesophylla macconnelli* ($2n = 21$ /males, 22/females; $FN = 24$). In addition, the sex-determining system appears to be similar (Baker et al., 1973). Baker (1973) proposed a line of evolution consisting of *Chiroderma*, *Vampyressa*, *Mesophylla*, and *Ectophylla* within the Stenoderminae, evolving from a theoretical primitive karyotype of $2n = 30$ or 32, $FN = 56$ or 60. Along this line, *V. pusilla* and *M. macconnelli* would be the karyotypically most derived species. Baker et al. (1973) modified this proposal, recognizing that *M. macconnelli* and the Colombian morph of *V. pusilla* have a similar sex-determining mechanism yet differ in cranial morphology and dentition. They postulated (p. 8) that these species evolved from a common ancestor with the derived sex-determining mechanism (where the Y has probably been translocated to an autosome) and the Central American karyotype has "undergone additional alterations that have resulted in a sex-determining system appearing as the classical XX/XY." Baker et al. (1973) proposed a closer relationship between *V. pusilla* and *M. macconnelli* than between *V. pusilla* and *V. nymphaea* or *V. brocki*.

Gardner (1977a:300-302) presented a third karyotype of *V. pusilla* from Perú with $2n = 22$ in males, 23 in females, and $FN = 22$ (Fig. 4). The chromosomes are described as follows: "Autosomes: 1 unpaired large metacentric and 9 pairs of medium-sized to small acrocentrics. The female has an additional pair of autosomes, the smallest in the complement, here considered to be acrocentric for the determination of FN, although each bears a very short second arm. The male possesses an unpaired acrocentric, which for descriptive purposes is considered with the sex chromosomes. Sex chromosomes: the X is considered to be a medium-sized subtelocentric because it is unpaired in the male and is comparable in size to the X in other *Vampyressa*. The male, in addition to the X and the small acrocentric mentioned previously, possesses a small submetacentric, which I presume represents the Y chromosome translocated to one of the smallest autosomes." It differs from the Colombian karyotype of Baker et al. (1973) by having a large, unpaired metacentric autosome and lacking one pair of acrocentrics. The unpaired chromosomes in males may differ slightly between the two chromosomal forms, but are essentially similar.

In his analysis of the evolution of *Vampyressa*, Gardner (1977a) noted that the range of diploid numbers in the subgenus *Vampyressa* is much larger than that in *Vampyriscus* (14 to 24 and 24 to 26, respectively) and that the fundamental number displayed by *Vampyressa* is at least one-half that of *Vampyriscus* (20 to 24 and 44 to 48, respectively). By plotting FN against $2n$, he derived a theoretical ancestral karyotype of $2n = 26$, $FN = 24$. From this karyotype, the Central American karyotype can be derived with two tandem and two Robertsonian fusions. Gardner (1977a) postulated that because this chromosomal configuration has a normal XX/XY arrangement, it must have developed before the South American karyotypes with multiple sex-determining mechanisms. The Colombian morph of *V. pusilla* can be derived with one tandem fusion and a Y-autosome fusion of the ancestral karyotype. The unpaired metacentric in the Peruvian form could be either a Robertsonian fusion or an isochromosome.

The generic phylogeny proposed by Gardner (1977a) is fundamentally different than that of Greenbaum et al. (1975), who postulated an ancestral karyotype of $2n = 30$, $FN = 56$, most similar to that of *V. nymphaea* ($2n = 26$, $FN = 48$). As Gardner (1977a) interpreted this, *V. brocki* ($2n = 24$, $FN = 44$) would have evolved from this karyotype with pericentric inversions of two autosomal chromosomes and a centric fusion. The Colombian form of *V. pusilla* then could have evolved with 11 additional pericentric inversions. Thus, the subgenus *Vampyriscus* would have been the predecessor of the nominate subgenus. Gardner (1977a) cited the retention of the maximum number of molars and incisors in *V. melissa* as evidence that from a morphological view, it is the least derived *Vampyressa* and argued that *Vampyressa* gave rise to *Vampyriscus*, rather than the reverse.

With Gardner's (1977a) theoretical ancestral karyotype, *V. melissa* ($2n = 14$, $FN = 24$) can be derived through a series of six Robertsonian fusions. *V. brocki* would have evolved through 11 inversions and one tandem fusion. *Vampyressa nymphaea* can be derived with 12 inversions.

Gardner (1977a) also doubted the close relationship between *V. pusilla* and *Mesophylla macconnelli* as proposed by Baker et al. (1973). His argument was that this close relationship would imply either the inclusion of *Mesophylla* in the genus *Vampyressa*, at least as a subgenus, or formation of three genera: *Vampyressa*, including *pusilla* and *melissa*; *Vampyriscus*, including *nymphaea*, *bidens*, and *brocki*; and *M. macconnelli*. The close morphological similarities among species included in the genus *Vampyressa* do not support either option. Gardner (1977a) stated that it is premature to grant a close relationship between *V. pusilla* and *M. macconnelli* on the basis of chromosomal similarities until the evolution of the sex-determining system is better understood.

Myers et al. (1983) reported the karyotype of three specimens of *V. p. pusilla* from Paraguay as $2n = 20$ and $FN = 36$. This karyotype is distinct from any of those reported for *V. p. thyone*. The sex-determining system was not described.

REMARKS. Peterson (1968) recognized three subgenera in *Vampyressa*, with *V. bidens* in the subgenus *Metavampyressa* on the basis of having only one lower incisor on each side. Davis (1975) found a variable number of lower incisors in the population of *V. bidens* he studied and questioned their separation into a distinct subgenus. He recommended that *Metavampyressa* be considered a junior synonym of *Vampyriscus*.

Baker et al. (1973) did not recognize subspecies in *Vampyressa pusilla* on the basis of karyotypic and morphometric data. All of the localities they studied, however, (Colombia, Honduras, Nicaragua, Ecuador, Venezuela, and Panamá) were in the range that Peterson (1968) cites for *V. p. thyone*. No specimens from Paraguay or Brazil, the range of the nominate subspecies, were examined. Myers et al. (1983) reported a karyotype for three specimens from Paraguay (*V. p. pusilla*) unlike any known from *V. p. thyone*.

The name *Vampyressa* is derived from the Serbian *Wampira* and literally means small vampire. This comes from the propensity of early naturalists to regard all Neotropical bats as vampires. *Pusilla* is from the Latin *pusillus* meaning small or petty.

LITERATURE CITED

- AELLEN, V. 1970. Catalogue raisonné des chiroptères de la Colombie. Rev. Suisse Zool., 77:1-37.
- ARMSTRONG, D. M. 1969. Noteworthy records of bats from Costa Rica. J. Mamm., 50:808-810.
- BAKER, R. J. 1973. Comparative cytogenetics of the New World leaf-nosed bats (Phyllostomatidae). Periodicum Biol., 75:37-45.
- BAKER, R. J. ET AL. 1973. Cytotypes and morphometrics of two phyllostomid bats, *Micronycteris hirsuta* and *Vampyressa pusilla*. Occas. Papers Mus., Texas Tech Univ., 17:1-10.
- BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. Bull. Florida State Mus., Biol. Sci., 24:359-408.
- BRENNEN, J. M., AND J. T. REED. 1975. A list of Venezuelan chiggers, particularly of small mammalian hosts (Acarina: Trombiculidae). Brigham Young Univ. Sci. Bull., 20:45-75.
- BRENNEN, J. M., AND C. E. YUNKER. 1966. The chiggers of Panama (Acarina: Trombiculidae). Pp. 221-266, in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, 861 pp.
- DAVIS, W. B. 1975. Individual and sexual variation in *Vampyressa bidens*. J. Mamm., 56:262-265.
- DAVIS, W. B., AND J. R. DIXON. 1976. Activity of bats in a small village clearing near Iquitos, Peru. J. Mamm., 57:747-749.
- DAVIS, W. B., D. C. CARTER, AND R. H. PINE. 1964. Noteworthy records of Mexican and Central American bats. J. Mamm., 45:375-387.
- FLEMING, T. H., E. T. HOOPER, AND D. E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. Ecology, 53:555-569.
- FORMAN, G. L. 1971. Histochemical differences in gastric mucus of bats. J. Mamm., 52:191-193.
- . 1973. Studies of gastric morphology in North American Chiroptera (Emballonuridae, Noctilionidae, and Phyllostomatidae). J. Mamm., 54:909-923.
- FURMAN, D. P. 1966. The Spinturnicidae mites of Panama (Acarina: Spinturnicidae). Pp. 125-166, in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, 861 pp.
- GARDNER, A. L. 1977a. Chromosomal variation in *Vampyressa* and a review of chromosomal evolution in the Phyllostomidae (Chiroptera). Syst. Zool., 26:300-318.
- . 1977b. Feeding habits. Pp. 293-350, in Biology of bats of the New World family Phyllostomatidae. Part II (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 13:1-364.
- GOODWIN, G. G. 1963. American bats of the genus *Vampyressa*, with the description of a new species. Amer. Mus. Novitates, 2125:1-24.
- GRAHAM, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. J. Mamm., 64:559-571.
- GREENBAUM, I. F., R. J. BAKER, AND D. E. WILSON. 1975. Evolutionary implications of the karyotypes of the stenodermine genera *Arlops*, *Ariteus*, *Phyllops*, and *Ectophylla*. Bull. S. California Acad. Sci., 74:156-159.
- HALL, E. R., AND W. B. JACKSON. 1953. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. Univ. Kansas Publ., Mus. Nat. Hist., 5:641-646.
- HANDLEY, C. O., JR. 1966. Checklist of the mammals of Panama. Pp. 753-795, in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, 861 pp.

- . 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young Univ. Sci. Bull., Biol. Ser., 20:1-91.
- HILL, J. E., AND J. D. SMITH. 1984. Bats: a natural history. Univ. Texas Press, Austin, Texas, 243 pp.
- HOWELL, D. J., AND D. BURCH. 1974. Food habits of some Costa Rican bats. Rev. Biol. Trop., 21:281-294.
- JONES, J. K., JR., J. D. SMITH, AND H. H. GENOWAYS. 1973. Annotated checklist of mammals of the Yucatan Peninsula, Mexico. I. Chiroptera. Occas. Papers Mus., Texas Tech Univ., 13:1-31.
- JONES, J. K., JR., J. D. SMITH, AND R. W. TURNER. 1971. Noteworthy records of bats from Nicaragua, with a checklist of the chiropteran fauna of the country. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 2:1-35.
- KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. Amer. Mus. Novitates, 2651:1-33.
- LAVAL, R. K., AND H. S. FITCH. 1977. Structure, movements and reproduction in three Costa Rican bat communities. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 69:1-28.
- MCDANIEL, V. R. 1976. Brain anatomy. Pp. 147-200, in Biology of bats of the New World family Phyllostomatidae. Part I (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 10:1-218.
- MILLER, G. S., JR. 1907. The families and genera of bats. Bull. U.S. Natl. Mus., 57:1-282.
- . 1912. A small collection of bats from Panama. Proc. U.S. Natl. Mus., 42:21-26.
- MYERS, P., R. WHITE, AND J. STALLINGS. 1983. Additional records of bats from Paraguay. J. Mamm., 64:143-145.
- PETERSON, R. L. 1965. The genus *Vampyressa* recorded from British Honduras. J. Mamm., 46:676.
- . 1968. A new bat of the genus *Vampyressa* from Guyana, South America, with a brief systematic review of the genus. Life Sci. Contrib., Royal Ontario Mus., 73:1-17.
- RAMÍREZ-P., J. R. ET AL. 1983. Lista y bibliografía reciente de los mamíferos de México. Univ. Auton. Metropolitana, Iztapalapa, pp. 1-363.
- REED, J. T., AND J. M. BRENNAN. 1975. The Subfamily Leeuwenhoekinae in the Neotropics (Acarina: Trombiculidae). Brigham Young Univ. Sci. Bull., 20:1-42.
- RICK, A. M. 1968. Notes on bats from Tikal, Guatemala. J. Mamm., 49:516-520.
- SMITH, J. D., AND A. STARRETT. 1979. Morphometric analysis of chiropteran wings. Pp. 229-316, in Biology of bats of the New World family Phyllostomatidae, Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16:1-441.
- STARRETT, A., AND L. DE LA TORRE. 1964. Notes on a collection of bats from Central America, with the third record for *Cyrtarops alecto* Thomas. Zoologica, 49:53-63.
- STUDIER, E. H., AND D. E. WILSON. 1983. Natural urine concentrations and composition in Neotropical bats. Comp. Biochem. Physiol., 75A:509-515.
- TADDEI, V. A. 1979. Phyllostomidae (Chiroptera) do norte-occidental do estado de São Paulo. III. Stenodermatinae. Ciência e Cultura, 31:900-914.
- THOMAS, O. 1900. Descriptions of new Neotropical mammals. Ann. Mag. Nat. Hist., ser. 7, 5:269-274.
- . 1909. Notes on some South-American mammals, with descriptions of new species. Ann. Mg. Nat. Hist., ser. 8, 4: 230-242.
- . 1924. On a collection of mammals made by Mr. Latham Rutter in the Peruvian Amazons. Ann. Mag. Nat. Hist., ser. 9, 13:530-538.
- TIMM, R. M. 1984. Tent construction by *Vampyressa* in Costa Rica. J. Mamm., 65:166-167.
- VALDEZ, R., AND R. K. LAVAL. 1971. Records of bats from Honduras and Nicaragua. J. Mamm., 52:247-250.
- WAGNER, J. A. 1843. Diagnosen neuer Arten brasilischer Handflüger. Archiv für Naturgeschichte, 9:365-368.
- WEBB, J. P., JR., AND R. B. LOOMIS. 1977. Ectoparasites. Pp. 57-119, in Biology of bats of the New World family Phyllostomatidae. Part II (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 13:1-364.
- WENZEL, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young Univ. Sci. Bull., 20:1-177.
- WENZEL, R. L., V. J. TIPTON, AND A. KIEWLICZ. 1966. The streblid batflies of Panama (Diptera: Streblidae). Pp. 405-676, in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, 861 pp.
- WILSON, D. E. 1979. Reproductive patterns. Pp. 317-378, in Biology of bats of the New World family Phyllostomatidae. Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16:1-441.

Editors of this account were B. J. VERTS and J. KNOX JONES, JR. Managing editor was CARLETON J. PHILLIPS.

S. E. LEWIS, JOSEPH MOORE MUSEUM, EARLHAM COLLEGE, RICHMOND, INDIANA 47374, AND D. E. WILSON, U.S. FISH AND WILDLIFE SERVICE, NATIONAL MUSEUM OF NATURAL HISTORY, WASHINGTON D.C. 20560.